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The Scope of Published Population Genetic Data for Indo-Pacific Marine Fauna and Future Research Opportunities in the Region

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Recommended Citation

Keyse, J., Crandall, E.D., Toonen, R.J., Meyer, C.P., Trembl, E.A., and C.R. Riginos. 2014. The scope of published population genetic data for Indo-Pacific marine fauna, and future research opportunities. *Bulletin of Marine Science* 90(1): 47-78.

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The scope of published population genetic data for Indo-Pacific marine fauna and future research opportunities in the region

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ABSTRACT.—Marine biodiversity reaches its pinnacle in the tropical Indo-Pacific region, with high levels of both species richness and endemism, especially in coral reef habitats. While this pattern of biodiversity has been known to biogeographers for centuries, causal mechanisms remain enigmatic. Over the past 20 yrs, genetic markers have been employed by many researchers as a tool to elucidate patterns of biodiversity above and below the species level, as well as to make inferences about the underlying processes of diversification, demographic history, and dispersal. In a quantitative, comparative framework, these data can be synthesized to address questions about this bewildering diversity by treating species as “replicates.” However, the sheer size of the Indo-Pacific region means that the geographic and genetic scope of many species’ data sets are not complementary. Here, we describe data sets from 116 Indo-Pacific species (108 studies). With a mind to future synthetic investigations, we consider the strengths and omissions of currently published population genetic data for marine fauna of the Indo-Pacific region, as well as the geographic and taxonomic scope of the data, and suggest some ways forward for data collection and collation.

Date Submitted: 2 January, 2013.

Date Accepted: 1 July, 2013.

Available Online: 18 November, 2013.

The waters of the Indian and Pacific oceans contain the greatest concentration of tropical marine biodiversity on Earth (Ekman 1953, Briggs 1974, Veron 1995). The question of why marine biodiversity is concentrated in this region, particularly at the juncture of the Indian and Pacific oceans, has been the topic of much study (Forbes 1856, Ekman 1935, Ladd 1960, Briggs 1974, 1999, Bellwood and Hughes 2001, Connolly et al. 2003, Carpenter and Springer 2005, Hoeksema 2007, Reaka et al. 2008, Renema et al. 2008, Bellwood et al. 2012). Tools from population genetics and phylogeography can enhance our understanding of how biodiversity is created and maintained in this region (Avice et al. 1987, Palumbi 1997, Barber and Bellwood 2005). Moreover, genetic approaches are essential for initial detection of the many cryptic species that apparently exist in this region (Knowlton 2000, Meyer et al.

Edited by Managing Editor Rafael J Araújo

2005, Barber and Boyce 2006, Vogler et al. 2008, Bowen et al. 2013) and can also be used to guide conservation (Moritz 1994, Moritz and Faith 2002, Rocha et al. 2007, Beger et al. 2014, von der Heyden et al. 2014).

Numerous studies have investigated population genetic and phylogeographic patterns in the Indo-Pacific region (for examples, see recent reviews by Crandall et al. 2008a, Carpenter et al. 2011, Toonen et al. 2011); however, the high levels of biodiversity, combined with the vast area of the Indian and Pacific oceans, poses substantial challenges for documenting spatial genetic patterns, much less inferring underlying processes. For instance, the coral reefs of eastern Indonesia, Malaysia, the Philippines, Papua New Guinea, East Timor, and the Solomon Islands (collectively referred to as the Coral Triangle), contain the world's greatest concentration of marine species, which is consistently estimated in the upper decile for most coastal marine taxa (Roberts et al. 2002, Carpenter and Springer 2005, Tittensor et al. 2010). Together, the Indian and Pacific oceans span two thirds of the globe, with most individual species ranges encompassing much of one or both ocean basins (Connolly et al. 2003). This area includes more than 65 nations of which 18 are classified by the UN as Least Developed Countries, and only four are classified as High Income Organisation for Economic Co-operation and Development (OECD) countries (<http://www.data.worldbank.org>, accessed December 2012).

Thus, population genetic surveys in the Indo-Pacific region are likely to involve fieldwork in locations that are distant from each other, potentially difficult to access, may be in developing countries, and will fall under diverse regulations and jurisdictions. These are significant logistical impediments for biological research. Moreover, with such high biodiversity, the degree to which one or a few species can represent entire communities is unknown, and recent studies argue against exemplar species representing patterns for the broader community (Bird et al. 2007, Toonen et al. 2011). In the face of such challenges, progress can be fostered if data are shared and properly catalogued in the interests of capturing emergent patterns in this complex system. Our purpose here is not to provide a review of previous work on genetic patterns in the region (see Palumbi 1994, Benzie 1998, Carpenter et al. 2011, Toonen et al. 2011 for examples focusing on particular regions within the Indo-Pacific). Rather, our goal is to provide a detailed overview of published data from population genetic studies of Indo-Pacific marine fauna, which could be used for synthetic studies. In addition, we aim to inform future empirical studies by determining the scope, strengths, and omissions of collective work to date, considering both the geographic and taxonomic coverage. Finally, we discuss potential uses for these published data that could provide a basis for future synthetic work and suggest guidelines for the collation of such data and future empirical investigations. The 108 studies presented here are the product of many years' work by many researchers and, if consolidated, would provide a solid foundation for our understanding of processes generating biodiversity in the region. Here we attempt to aggregate these efforts, identify significant areas of overlap or gaps, and suggest a standard platform for synthesis and collaboration.

METHODS

A literature search was conducted using Web of Science™ (Thomson Reuters) on 21 June, 2012. The search terms were chosen to maximize inclusion of articles

containing georeferenced data on population genetic diversity from shallow water marine habitats in the Indo-Pacific region. The following sets of Boolean search terms were combined in the Advanced Search tool: (1) gene flow OR population structure OR genetic diversity OR phylogeograph* OR F statistic OR mtDNA OR microsatellite OR allozyme, AND (2) Marine OR coral OR reef OR intertidal OR subtidal OR estuar*, AND (3) Indo* OR Malay* OR Indo-Pacific OR Coral Triangle. The titles and abstracts of all papers were assessed and articles that did not fit the following criteria were discarded: (1) only marine animals; (2) only tropical Indo-Pacific studies bounded by the geographical limits of north to Tropic of Cancer (30°N), south to Tropic of Capricorn (30°S), west to Cape Town, South Africa (20°E), and east to the Eastern Pacific Barrier (125°W); (3) only data based on DNA sequences, microsatellites or allozymes; (4) at least three populations were sampled per included study; (5) at least five individuals from a population had to be sampled for that population to be included; (6) the study had to provide sample sizes and indices of genetic diversity at the population level; and (7) the study had to provide latitude and longitude or a map/description of the sampling sufficient to permit location of sampling sites to within 500 km.

Articles remaining in the data set after this first pass were more closely investigated (reading the text of the introduction, methods, results, or supplementary material) to assess their fit to these criteria. Details of the authors, year of publication, genetic marker, sample size, species name, and population geographic positions from articles meeting all criteria were recorded. These criteria targeted population genetic articles, so that purely phylogenetic studies were usually discarded due to low population number or sample sizes. The resulting list was checked by experts in the field attending a catalysis meeting at the National Evolutionary Synthesis Center (NESCent) on the “Molecular Ecology and Evolution of the Indo-Pacific” and some relevant papers not captured by the literature search were added.

All maps were produced in ArcMap (version 10, ESRI, Redlands, CA) using coastline data from the Global, Self-consistent, Hierarchical, High-resolution Shoreline Database (Wessel and Smith 1996). Geographic coverage of studies and species was estimated by measuring the area of a convex hull drawn around the point locations of each study or species. Probability-based species range maps were downloaded from Aquamaps (<http://www.aquamaps.org>). Sampling locality polygons were generated by buffering each data point by 60 km and dissolving to merge points close to each other. Species range polygons were drawn in ArcMap 10 using a convex hull of the occurrence points listed in the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>, accessed 13 November, 2012) supplemented by the genetic database points for each species and some points gleaned from the literature for those species not listed on GBIF. Two species [*Echinometra* sp. C (Uehara and Shingaki 1985) and *Euryhaliotrematoides grandis* (see Appendix 1 for species authorities)] were excluded from these analyses because occurrence data could not be found. The GBIF occurrence polygons were merged and joined with sampling locality polygons to generate a count of species for each locality. We then divided the number of species sampled by the total number from the data set present and converted to a percentage. We chose to standardize by the number of species from the dataset with ranges intersecting a location rather than attempting to derive species richness estimates because reliable estimates of species richness across the six phyla that our data set encompasses are difficult to make. The number of species sampled was also divided by total reef area

within each polygon to generate sampling per unit area of habitat. Statistical analyses were conducted in R statistical software (R Core Team 2012) and areas estimated by convex polygons were square-root transformed prior to analysis. We also performed a community-style cluster analysis using sampling localities as the groups of interest and sampled species as presence/absence information. Thus, inference from this cluster analysis is about sampling practices rather than actual community composition. We calculated Euclidean distances among sites with the *vegan* package for R (Oksanen et al. 2012) and clustered them into groups using Ward's Minimum Variance criterion.

RESULTS AND DISCUSSION

In total, 493 studies were returned from the initial Web of Science search. This number was reduced to 108 following application of the criteria given above (see Appendix 1). These 108 studies covered 116 species in six phyla. The data set contained 1451 genetic diversity data points, with each point representing a georeferenced collection of a given species (five or more individuals of that species) and genotyped by a category of marker (mtDNA sequencing, microsatellites, or allozymes). In the final data set, there were 725 different geographic locations in 50 different countries.

TAXONOMIC PATTERNS.—Among Indo-Pacific genetic studies, there was a clear bias toward ray-finned fishes; just over half (69 of 126) of all species studied were Actinopterygians. The remaining 57 studies surveyed were, in descending order of coverage: Mollusca (16 species), Arthropoda (11 species), Echinodermata (11 species), Cnidaria (4 species), other Chordata (2 species of reptile, 2 species of shark and 1 species of lancelet), and a single representative of the Platyhelminthes (Fig. 1). Thus, large and relatively firm-bodied taxa have been preferred, whereas speciose phyla such as Annelida, Cnidaria, and Porifera have been overlooked, perhaps due to difficulty in identification, preservation, or subsequent DNA amplification. Even the relatively well-studied Mollusca were under-represented in comparison to fishes when considering their proportional species richness in marine habitats [more than 40,000 estimated species of molluscs (WoRMS Editorial Board 2012) vs 16,764 of Actinopterygians (Eschmeyer et al. 2010)].

This large discrepancy in studies across phyla does not simply result from investigator bias. Invertebrates are generally more difficult to identify to the species level for the non-expert and molecular work is often challenging due to a paucity of genomic information for primer design (Toonen 1997, Fernandez-Silva et al. 2013). In addition, mucus and other polysaccharides commonly found in marine invertebrates are known to inhibit PCR (Huelsen et al. 2011, Vargas et al. 2012). Finally, anthozoans and sponges have a notorious deficiency of variation in their mitochondria (Shearer 2002, Hellberg 2006), such that this useful genetic marker is usually not informative for these taxa (but see Forsman et al. 2009), and development of nuclear markers has generally lagged far behind mtDNA (Karl and Avise 1993, Hare 2001, Puritz et al. 2012). Conversely, fishes are good candidates for population genetic and phylogeographic studies due to their varied life histories and functional traits and their many readily identifiable species. Genetic work tends to be easier in fishes, whose vertebrate affiliation and economic importance mean that there is a plethora of genetic information available for primer design. Despite this overall skew towards fishes,

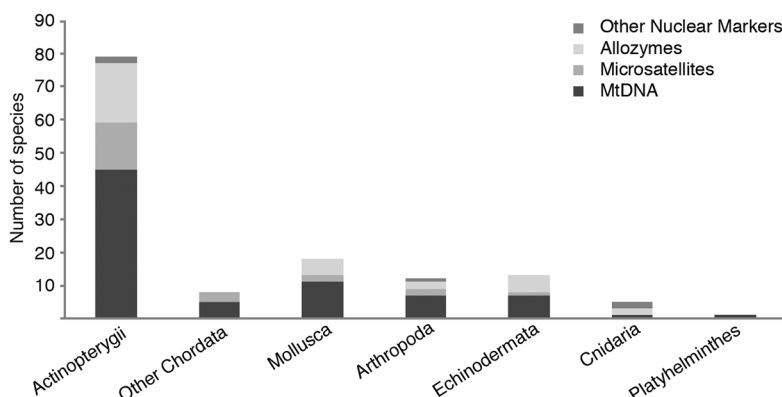


Figure 1. Histogram showing the number of taxa studied by the four categories of molecular marker type.

however, the top five most studied species in this data set (based on the number of published studies of that species and by the number of total geographic locations sampled for each species) consisted of four invertebrates and a single fish (discussed in detail in the Text Box, *see next page*).

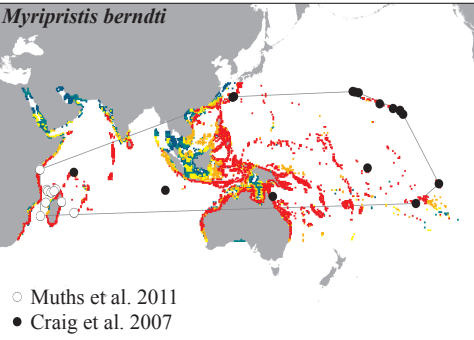
The bias toward Actinopterygii remains in multi-species studies. There are 19 studies in the final data set that include more than one species, of which 12 were of fishes (Doherty et al. 1995, Dudgeon et al. 2000, Fauvelot and Planes 2002, Drew et al. 2008, Magsino and Juinio-Meñez 2008, Ramon et al. 2008, Thacker et al. 2008, van Herwerden et al. 2009a, Gaither et al. 2010, Mirams et al. 2011, Lord et al. 2012, Ludt et al. 2012) and seven of invertebrates (Palumbi et al. 1997, Uthicke et al. 2001, Barber et al. 2002, Crandall et al. 2008a,b, Kochzius et al. 2009, Duda et al. 2012). Generally, studies include phylogenetically similar species (e.g., for fishes: Fauvelot and Planes 2002, Magsino and Juinio-Meñez 2008, Thacker et al. 2008, Lord et al. 2012, Ludt et al. 2012; and for invertebrates: Palumbi et al. 1997, Uthicke et al. 2001, Barber et al. 2002, Crandall et al. 2008a, Duda et al. 2012). However, an exception is that two multispecies studies have focused on the seastar *Linckia laevigata* and its gastropod parasite *Thyca crystallina* (Crandall et al. 2008b, Kochzius et al. 2009). The comparative context that is offered by multi-species studies is valuable to any attempt to establish general associations between genetic patterns and geography or biological traits (Bowen et al. 2014). It is hoped that future sampling efforts can be coordinated in such a way as to maximize the comparative value of data sets for individual species (see below).

GEOGRAPHIC SCOPE.—Given the vast area and logistical constraints to fieldwork in the Indo-Pacific, it is not surprising that few Indo-Pacific genetic studies encapsulate the entire geographic range of a species. We examined the geographic scope of studies using a variety of criteria: the geographic extent (area encompassed by sampling), the number of sampling sites, and the density of sampling locations within geographic extent (Fig. 2). The five species with the greatest geographic sampling extent are highlighted in the Text Box. A general perception of population genetic studies is that there is an inherent trade-off between the geographic extent of sampling and the number of sampling sites. That is, some sampling strategies might be expected to include geographically distant sites to maximize the geographic extent

▼ The top five species with greatest sampling extent

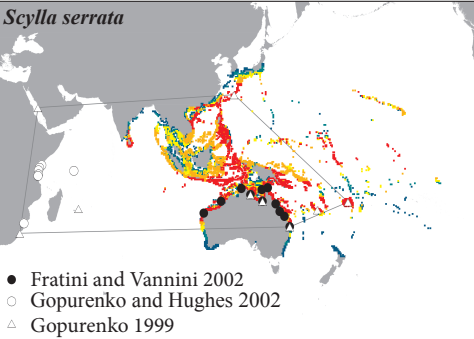
Species sampled across a wide area represent those for which broadscale patterns can be investigated. Heatmap colours show probabilistic occurrence from Aquamaps.org. Symbols show sampling events.

Myripristis berndti



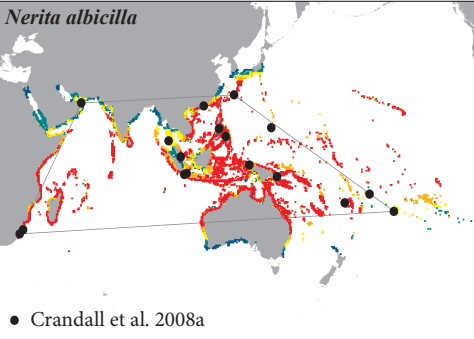
Myripristis berndti, the bigeye soldierfish, is the species with the widest geographic coverage. The species has been the focus of two population genetic studies: one study restricted to sites around Madagascar (Muths et al. 2011) using mtDNA (*cytochrome oxidase b*) and microsatellites and one study with sites in both the Indian and Pacific Oceans (Craig et al. 2007) using mtDNA (*cyt b*) alone, yet neither study included locations in the Coral Triangle. Extending future coverage to include the Coral Triangle would be an obvious next step for this species.

Scylla serrata



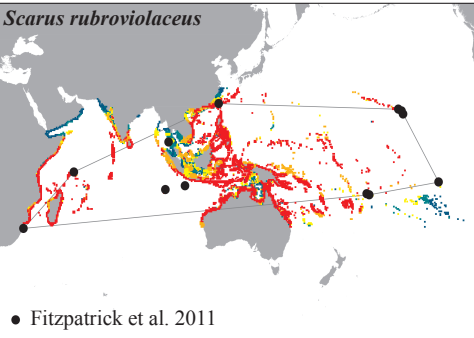
Scylla serrata, the mud crab, ranks second in the greatest geographic sampling extent. It has been the focus of three Indo-Pacific studies (Gopurenko 1999, Fratini and Vannini 2002, Gopurenko and Hughes 2002). Each employed mtDNA *COI*, so combination of the data is straightforward. For this reason, further studies on this species should include *COI* sequencing. With the exception of the Solomon Islands [Liu et al. 2007 (not captured by this search, part of a synthesis by Fratini et al., 2010)], there are no data for *S. serrata* from the Coral Triangle.

Nerita albicilla

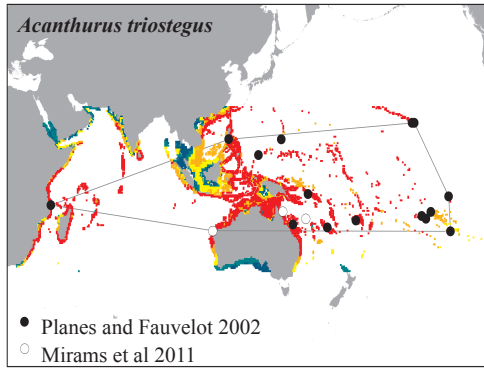


Nerita albicilla, an intertidal gastropod, is the species with the largest geographic coverage represented by a single study. Crandall et al. (2008a) included the species alongside its congener *Nerita plicata* in a comparative study that revealed markedly different patterns of genetic structure between these two closely related and ecologically similar species. It would seem that the majority of the species range has been covered by this study (and by Frey and Vermeij 2008, although this study was excluded from the dataset as it did not report genetic diversity data).

Scarus rubroviolaceus



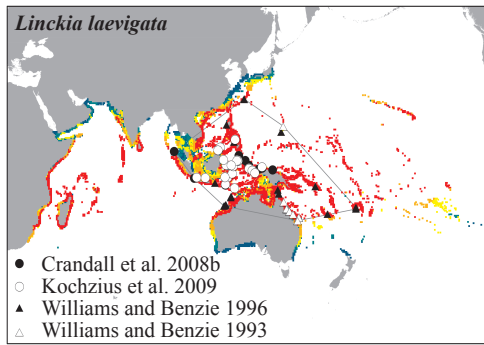
Scarus rubroviolaceus, the redlip parrotfish, has been surveyed from South Africa to the Marquesas within a single study. Fitzpatrick et al. (2011) used patterns of genetic structure in this species to distinguish between hypotheses explaining the diversity hotspot found in the Coral Triangle. The sampling in this study covered the edges of the species range fairly well, with the exception of the Coral Triangle itself. Sites in the Coral Triangle would enhance the understanding of processes behind patterns of high diversity at the juncture between the Indian and Pacific oceans.



Acanthurus triostegus, the convict surgeonfish, has a range spanning the Indian and Pacific oceans. This is the fifth widest sampled species included, with 7879 km² covered by two studies. Planes and Fauvelot (2002) used allozymes to assess population structure in the Pacific Ocean, but sampled only a single location in the Indian Ocean and none in the Coral Triangle. Mirams et al. (2011) used mtDNA (*COI*) to investigate the effect of the Torres Strait landbridge, sampling two sites in the Pacific Ocean and one in the Indian Ocean. The different molecular markers preclude combination of existing data, but there is scope for further sampling of the Indian Ocean and Coral Triangle.

▼ The top five species with the most locations sampled

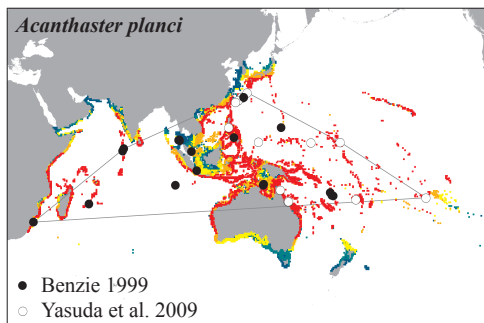
Species sampled from the highest number of locations represent those that may be a potentially fruitful focus for more geographically widespread sampling, even if individuals studies did not encompass a wide expanse of the ocean.



Linckia laevigata, the blue starfish, has been the focus of four studies covering 59 sites. *Linckia laevigata* and its parasite *Thyca crystallina* (Crandall et al. 2008b, Kochzius et al. 2009) were included in two mtDNA *COI* studies in the Coral Triangle. Two allozyme studies (Williams and Benzie 1993; 1996) sampled more widely, however there remains scope for work across the Indian and Pacific Oceans. Further work should include *COI* to allow data combination. A recent study has made a start on addressing this gap with *COI* sequences from Kenya and Madagascar (Otwoma 2012).

Scylla serrata, the mud crab, has been both densely and widely sampled (map shown opposite page). The density is due to it having been the focus of two fine scale studies in different oceans (Fratini and Vannini 2002; Gopurenko and Hughes 2002), which drives up the sampling location numbers and area of the species sampling polygon. There remains scope for further work on this species in the region.

Pterapogon kauderni, the Banggai cardinalfish (map not shown), is endemic to Indonesia and Malaysia. It has been the focus of three studies (Bernardi and Vagelli 2004, Hoffman et al. 2005, Vagelli et al. 2009) over most of its range, each using different markers. Further studies on other endemics could reveal mechanisms maintaining small ranges and genetic health of such species.



Acanthaster planci, the Crown of Thorns seastar, has been studied twice in the Indo Pacific (Benzie 1999, Yasuda et al. 2009) at 36 locations. The sampling of the above studies overlaps in the west Pacific but coverage is lacking in the rest of the Pacific. This gap is partially filled by two recent mtDNA papers in the Central Pacific (Timmers et al. 2011, 2012); however, the addition of mtDNA (*control region*) work on this species from the Indian Ocean and Coral Triangle would allow combination of these data.

Tridacna crocea, the boring giant clam, has been the focus of two studies at 35 sites in the Coral Triangle (DeBoer et al. 2008; Kochzius and Nuryanto 2008). Coverage in this region is substantial, but absent elsewhere in the species' range. There is wide opportunity for further work on *T. crocea*, particularly using mtDNA *COI* to fit with existing work and increase the geographic scope.

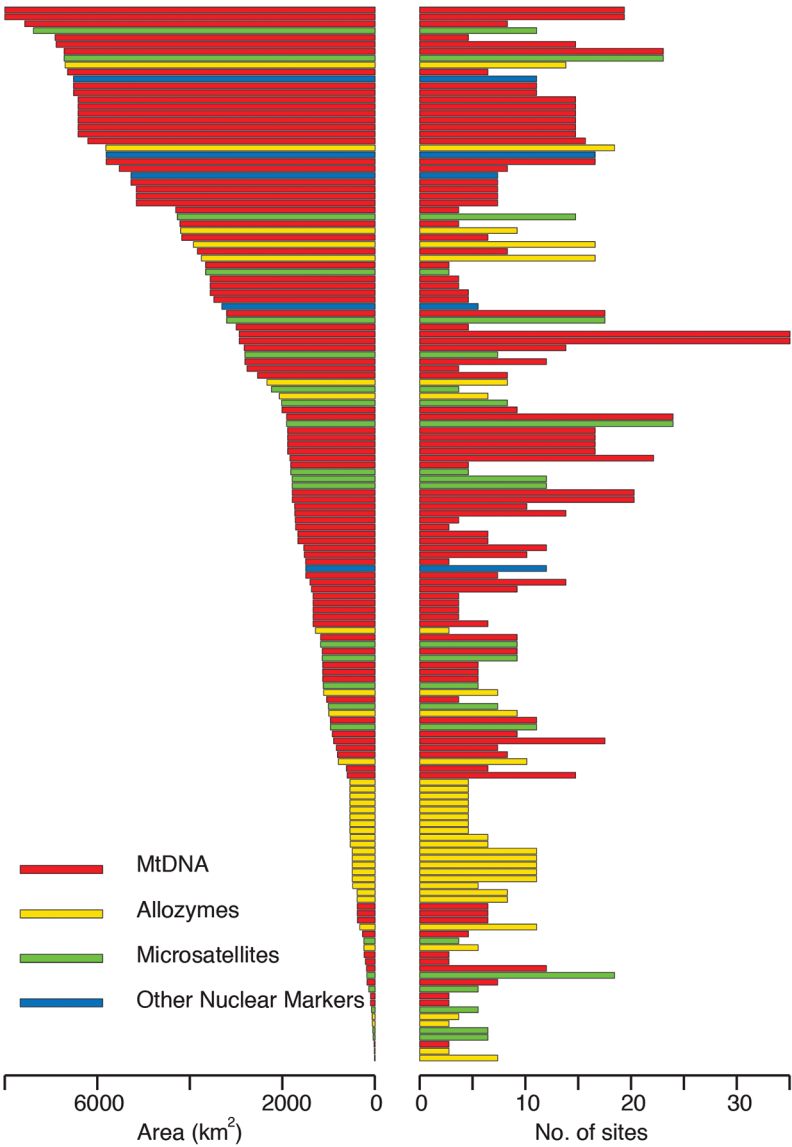


Figure 2. Summary of sampling for genetic surveys included in the present study. Total area surveyed (km²) and the number sites survey are indicated per species.

of the study but that the expense and logistics of widespread sampling would limit the total number of sites. Other studies might prioritize sampling density and limit themselves to a smaller geographic extent but include more total sites. In addition, it could be that studies of the latter type might preferentially use microsatellites so as to infer recent migration events.

These expectations, however, were not borne out. The area encompassed by individual studies varies widely from 14.8–9092 km² (with mean and median values of 2141 and 1892 km²) and the maximum number of sites is 38 (with a mean and median of 10.4 and 9 per study). There was a slight but significant positive relationship

between sampling area (i.e., geographic extent) and number of sites (that can be described by the equation: no. sites = $5.648 + 0.102 (\sqrt{\text{area}})$, $F_{1,150} = 24.96$, $R^2 = 0.143$, $P < 0.00001$, following removal of an outlier study (Johnson et al. 1994), which included eight sites over approximately 14 km². Sampling areas differ according to the genetic marker employed by each study (ANOVA: $F_{3,149} = 8.94$, $P < 0.0001$), with the greatest geographic extent for studies using “other” nuclear markers, followed by mtDNA sequences, microsatellites, and allozymes. The difference in area is only significant when comparing allozyme studies to either mtDNA sequence or “other” nuclear marker studies (Tukey’s post hoc tests: both $P < 0.004$). Thus, contrary to expectations, there was no significant difference in sampling area between microsatellite and mtDNA based studies. The number of sites surveyed had no effect on the choice of genetic marker (ANOVA: $F_{3,149} = 1.075$, $P = 0.361$). In summary, then, there was no evidence for trade-offs between sampling extent and number of sites among Indo-Pacific studies.

Two noteworthy studies illustrated the lack of inverse correlation between geographic extent of sampling and density of sampling locations. First, the study with the greatest geographical extent (9092 km²) explored the phylogeographic patterns of *Nerita albicilla* and *Nerita plicata*, two intertidal gastropods (Crandall et al. 2008a) and included a number of evenly-spaced sites (21 sites included in this database) spanning most of the species’ range (see Text Box). Second, the study with the maximum number of sampling locations (38 sites) encompassed 3336 km² of the Coral Triangle and provided comparative data for two closely related species of mantis shrimp (Barber et al. 2002). These two studies have both managed to achieve substantial geographic coverage alongside maintaining a high number of sampling locations and focusing on more than one species.

Another aspect of geographic sampling scope concerns the total number of sampling locations, especially combined across multiple studies. Species that have been included in multiple studies represent opportunities for collaboration and data synthesis, whereby the total geographic scope could be maximized. The five species with the greatest total number of sampling locations are discussed in the Text Box and represent opportunities for synthetic analyses. An extension of the total number of sampling locations is the density of sampling per species (total area covered / number sampling locations). While species with wide geographic sampling covering substantial portions of their range are important for revealing broadscale phylogeographic patterns, studies with dense sampling provide detailed knowledge of connectivity in a small area that may be particularly relevant to marine conservation management actions (Harrison et al. 2012). The top five species in terms of the density of sampling points were: *Craterocephalus capreoli*, *Pterapogon kauderni*, *Siganus guttatus*, *Chromis atripectoralis*, and *Stegastes nigricans*. Such data sets can complement wide-ranging data sets by illuminating population genetic patterns at a small scale but the direct applicability of their findings is necessarily limited to the region in question.

IDENTIFYING ANCHOR LOCATIONS.—Given the many difficulties associated with field work in the Indo-Pacific region, it might be expected that researchers would choose to sample in places they or colleagues have sampled before, that are easy to access, or might have colleagues collect for them to reduce the costs. These locations might be established marine stations run by universities or non-governmental

organizations, or they may simply be places where a “pioneer” researcher has established a connection and opened up the way for other researchers to follow. This would lead to a pattern of a few sites being the focus of multiple studies on multiple species. From the perspective of future work in the region, such sites can provide “anchor” locations with which direct comparisons can be made among taxa and studies, and therefore their inclusion might be prioritized in future empirical research projects.

Most of the point locations sampled to date were represented for only one species (484 locations out of a total of 682 locations) or by one study (490 locations); however, several localities stand out for the number of species sampled there. Localities are defined here as the polygons created by buffering each data point by 60 km and dissolving to merge points close to each other into a single locality. Figure 3 illustrates these patterns of uneven sampling across the Indo-Pacific region. Figure 3A shows localities colored according to the number of species that have been sampled as a proportion of those species in the data set with ranges intersecting that locality. The Society Islands, the Marquesas, and Main Hawaiian Islands in the central Pacific are localities where sampling has been high relative to the number of species occurring there (>40% of species from the dataset have been sampled). Other potential “anchor” localities identifiable from Figure 3A are the Northern Great Barrier Reef (GBR), Okinawa, Marutea Atoll in the central Pacific, and Pearl and Hermes Atoll in the Northwestern Hawaiian Islands. However, when the percentage of species sampled in a locality is divided by the area of the locality polygon, we can see patterns of coverage per unit area (Fig. 3B). After this correction has been made, Rangiroa, Takapoto, and Kiritimati in the central Pacific, along with the Seychelles, Christmas Island, and Cocos-Keeling Island in the Indian Ocean emerge as important nodes. Not surprisingly, the GBR localities fade in their influence due to the large area they encompass. Nevertheless, the dense sampling within the GBR, as evidenced by the sizes of the polygons resulting from buffering of point locations, and the relative ease of accessibility of remote reefs here, argues for its inclusion in any list of target locations.

CO-SAMPLED LOCALITIES.—The above section illustrates that sampling effort has been uneven across the Indo-Pacific region, with some locations attracting more sampling events than others. Here we investigate whether certain sites are commonly co-sampled, such as might be expected from a situation of reusing the same anchor locations, combining the sampling of many species in a single sampling expedition, or planned multispecies investigations. Figure 4 shows this tendency for subsets of locations to be co-sampled across species. The Hawaiian islands locations form a single cluster (yellow in online version) reflecting the many studies that have sampled multiple locations within Hawaii. Similarly, sites from the Coral Triangle form a distinct cluster (blue in online version). The Great Barrier Reef (green in online version) is strikingly unconnected to other localities, indicative of many studies that have sampled within the GBR only and not included additional locations. Conversely, a suite of isolated oceanic islands from both the Pacific and Indian oceans (red in online version) have been intensely co-sampled despite their geographic breadth (the Seychelles to the Marquesas, >165° of longitude).

These clusters of sampling effort highlight opportunities for multispecies syntheses (within sampling blocks), but also show how the currently available data limit

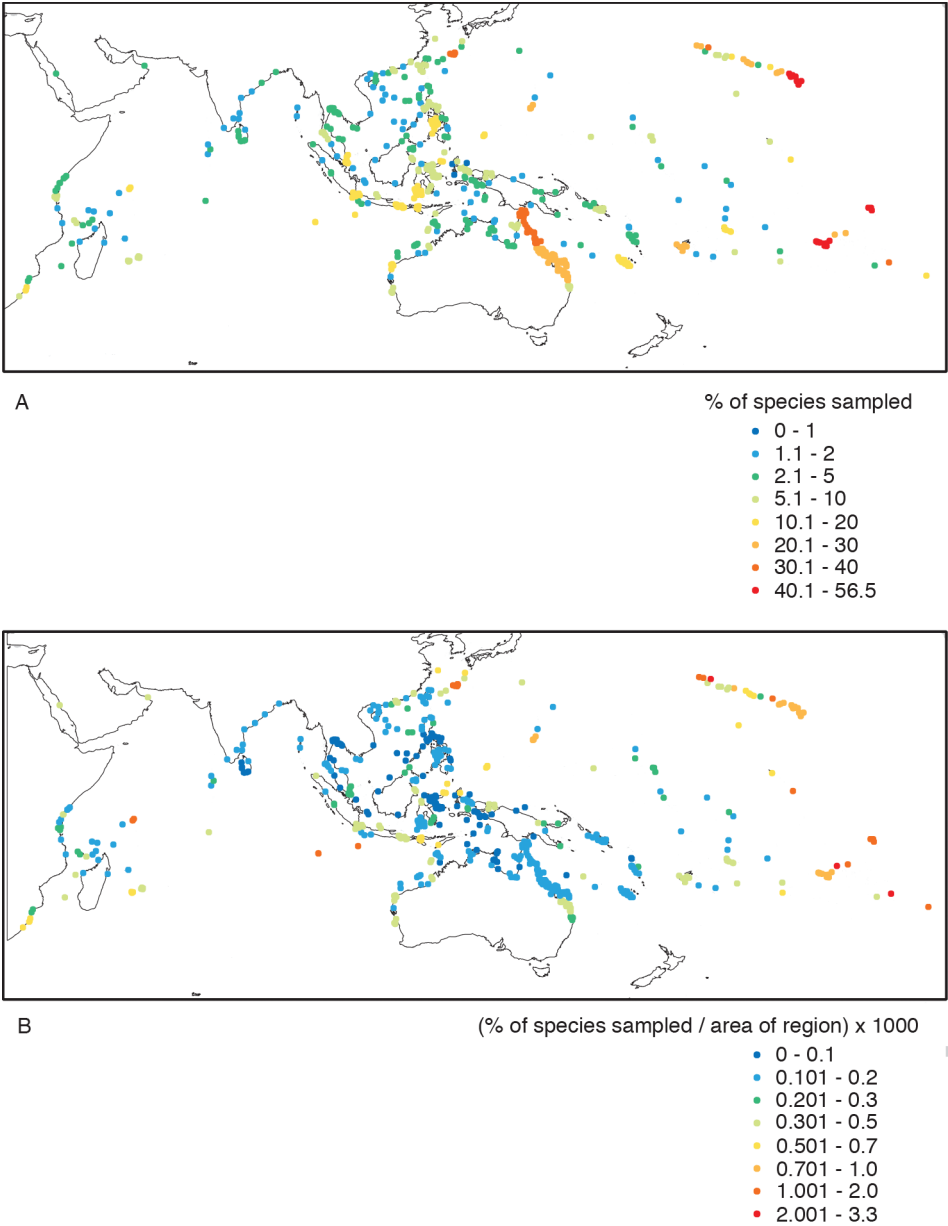


Figure 3. (A) Sampling intensity for the 116 species surveyed. A heatmap colored by the proportion of studied species is shown per site with a correction for species range. For example, from the main Hawaiian Islands, 22 species have been surveyed and 39 species from the 116 in the data set have species ranges that encompass this location, which gives a percentage of 56.4. (B) Sampling intensity for the 116 species corrected for the area of the study locality. As the locality polygons are of different area depending on the proximity of sampling locations, this correction allows us to see intensity of sampling per unit area. For example, the Main Hawaiian Islands locality has an area of 69,063 km², so the corrected sampling intensity is 56.4 / 69,063 or 0.0008.

Sequence based markers are especially amenable for combining data sets, provided that different studies target the same locus. Markers based on fragment size or charge differences (microsatellites and allozymes, respectively) are not directly comparable across research groups without sharing standards (such as tissues genotyped by each group to form a common frame of reference). Therefore, microsatellite and allozyme studies are often limited to stand-alone examples of genetic patterns for a particular species. Regardless of the marker used, qualitative patterns of divergence can be recognized, however, quantitative analyses rely on data produced from the same marker to control for different mutation rates. Sequence data can be exchanged with fewer concerns about reliability, and most studies currently upload their edited sequences to public repositories [e.g., NCBI Genbank (<http://www.ncbi.nlm.nih.gov/genbank>), EMBL-Bank (<http://www.ebi.ac.uk/embl>), and the DNA Data Bank of Japan (<http://www.ddbj.nig.ac.jp>)]. Thus, the growing collection of mtDNA sequence data is a valuable public resource for the Indo-Pacific research community. However, these data are most useful to other researchers when properly georeferenced (see best practice recommendations below). As a measure of the current standard of georeferencing, 20 studies were excluded from the data set owing to vague reporting of geographical locations. If a population sampling location could not be identified to within approximately 500 km the location was excluded from the dataset; this resulted in 19 data points covering nine species in 10 localities being excluded from the set of accepted studies.

The emergence of several DNA barcoding initiatives in recent years has led to the gathering of large volumes of mtDNA sequence data for the purposes of identification and cataloguing of biodiversity. DNA barcoding involves the sequencing of a common gene that is informative of species-level differences; the accepted barcode for most animals is a fragment of the mitochondrial COI gene. Global marine barcoding projects include Barcode of Life Datasystems (BOLD), Tree of Life, FishBOL, MarBOL, CnidToL, and the Sponge Barcode Project. When the data from these initiatives are made public, they will greatly increase the geographic and taxonomic scope of available mtDNA COI data. This further argues for the inclusion of this locus in population genetic studies in the region.

RECOMMENDATIONS FOR FUTURE WORK

DATA SYNTHESIS AS AN APPROACH FOR UNDERSTANDING INDO-PACIFIC BIODIVERSITY.—Greater knowledge regarding the spatial genetics of Indo-Pacific taxa will inform long-standing questions regarding the origin and dynamics of marine biodiversity in the Indian and Pacific oceans. Simply put, these oceans are far too large and their communities far too diverse for any single research group to empirically summarize spatial genetic diversity. Only by combining data across locations and taxa can broadscale emergent patterns be identified. For instance, where are the geographic locations of genetic disjunctions and how do they differ among species? Are there biological traits that influence the permeability of a barrier to gene flow? In the Coral Triangle, at the juncture of the Indian and Pacific oceans, there appear to be many instances of genetic breaks (Carpenter et al. 2011), but how such barriers differ among taxa is poorly resolved. Conversely, within the Hawaiian Archipelago, concordant genetic breaks are observed across broad taxonomic lines that are not obvious from any of the single-species studies to date (Toonen et al.

2011). Competing hypotheses regarding broadscale patterns of species diversity (Bellwood et al. 2012) invoke asymmetric migration or colonization. Population genetics provides tools to estimate these asymmetries and this could be done for many taxa. While the main objective of the present study has been toward compiling studies listing genetic diversity data, the practice of using phylogenies combined with information about range size and location alongside species traits has been gaining ground in recent years (Meyer 2003, Paulay and Meyer 2006, Selkoe et al. 2010, Choat et al. 2012). These recent papers provide examples of the kind of synthetic work that can be done with existing data to make sense of the bewildering array of biodiversity in the Indo-Pacific region.

Traditional population genetic reviews have been based on qualitative assessment of published works, which are being complemented by a growing literature using quantitative tests of specific hypotheses (examples from the Indo-Pacific region include: Meyer 2003, Lessios and Robertson 2006, Paulay and Meyer 2006, Hickerson and Meyer 2008, Crandall et al. 2012), and some rely upon reusing previously published data (Bradbury and Bentzen 2007, Weersing and Toonen 2009, Mirams et al. 2011, Riginos et al. 2011, Selkoe and Toonen 2011). Multiple-species studies are essential for addressing questions about how geography and biological traits affect genetic diversity and partitioning, as species are the unit of replication. Concordant patterns among species support scenarios whereby shared geographic features contribute to similar population genetic structure (Avice 2000), and comparisons among closely related taxa can reduce evolutionary variance when searching for commonalities or points of contrast between species (Dawson 2012). Many research programs are purposefully co-sampling numerous taxa, although the theory for simultaneous statistical evaluation of multiple species is not well developed (see Hickerson and Meyer 2008 for an important exception and example).

Thus, the potential value of any single study exceeds one or two standalone publications. The value of such data synthesis is becoming apparent across the fields of ecology and evolutionary biology and, concurrently, a cultural shift is underway whereby many funding bodies (including the National Science Foundation in the USA, the National Environment Research Council in the UK, and the Deutsche Forschungsgemeinschaft in Germany) and journals (see <http://www.datadryad.org/pages/jdap> for a list of journals in evolution and ecology) are requiring that raw data be accessible. Ensuring raw data are made public provides direct benefits to the scientific community, including long-term preservation, verifiability, and availability for data reuse (Tenopir et al. 2011, Whitlock 2011), and also to the publishing author, as citation rates are higher for papers that make their data available (Whitlock 2011). Despite this apparent shift, there are no official guidelines or consensus as to what constitutes essential data elements for population genetics so that what is reported across studies varies widely.

BEST PRACTICES FOR REPORTING POPULATION GENETIC DATA.—Here, we outline the minimal scope of a population genetic survey and the aspects of data that should be reported for Indo-Pacific studies to maximize the continued utility of published work to the scientific community. We recommend that a population genetic survey include an absolute minimum of three populations to allow partitioning of diversity among locations. Whereas in this survey we include studies sampling as few as five individuals per population in the interests of representing a full range of studies, we

believe that targets of at least 15 individuals per population for mitochondrial sequence data and 20 for microsatellites and SNPs would provide reasonable estimates of diversity by location. Data reporting should include the latitude and longitude of each sampled population with a detailed map as a beneficial complement. Dates of collections are essential to allow the consideration of temporal change.

In addition to the sample size and exact sampling locations, our opinion is that a population genetic study should report frequently used summary statistics that provide commonality across studies. This includes reporting diversity per location [haplotype diversity (h) and average pairwise differences (π) for sequence data, allelic diversity/number of alleles (A) for microsatellites, minor allele frequency for SNPs, and both observed (H_O) and expected (H_E) heterozygosity for genotype data]. Authors should also report measures of population differentiation (with F -statistics being the most commonly reported differentiation statistics). Although reporting of F -statistics has differed based on data type (G_{ST} and similar statistics being used for genotype data, and N_{ST} statistics for sequence data), recent work has identified the need to consider allelic diversity (Hedrick 2005) so that metrics correcting for this diversity might be in order (see Bird et al. 2011 for an extended discussion). Neutrality test scores for sequence data are also useful, with Tajima's D and F_s (Tajima 1989, Fu 1997) being commonly used, though there is disagreement about the suitability of current null models for mitochondrial sequence data (Wares 2009). If nothing more, the diversity of possible estimators underscores the necessity of making all raw data available so that new approaches can be applied to old data.

Edited, georeferenced sequence data of unique haplotypes should be accessioned at NCBI, EMBL, or DDBJ and accession numbers reported. Unedited, georeferenced sequences (e.g., FASTA files) for all individuals, along with input files for all reported statistics (e.g., NEXUS, XML, or .parm files, etc.), should be deposited in a flexible online data repository such as Dryad (<http://www.datadryad.org>) for studies to be fully transparent and repeatable. Many studies (examples include work from some of the authors on this paper) only take partial steps toward such accessioning, such as depositing sequences of unique haplotypes only or labeling accessions in a manner whereby the geographic origins are unclear.

For multilocus genotype data, ideally full genotypes of all individuals should be made available and their geographic origins explicit. However, there is no easily searchable public repository designed for such data at present. The creation of a shared database including all Indo-Pacific population genetic data would allow such data to be housed and, if integrated with a collaborative online research forum, would facilitate further progress in the field. Until such infrastructure exists, placing full georeferenced genotype information in Dryad or appending files as supplements to the published paper would represent best practice. Because sequence data, especially from mtDNA, can be readily consolidated among research groups (see previous section), there is a distinct advantage to including mtDNA sequences as part of all future genetic surveys.

While the above practices will help maintain consistency across population genetic studies and facilitate collation of data, sampling for these studies also yields data useful to users outside the field of molecular ecology. For example, the locations of sampled populations can add data to occurrence databases for the species, allowing refinement of species range maps and the mapping of species richness patterns. At present, there is a notable mismatch between the locations of occurrence data points

held in GBIF and those for the same species from population genetic studies; this can be easily solved by integrating these useful online repositories.

The recommendations laid out in this final section are likely to be familiar to most readers; we are not suggesting a major shift, merely a strengthening of the system already in place and the potential addition of more streamlined workflows. In an age where genetic data are increasingly numerous and funding agencies are increasingly frugal, we have a responsibility to make the most out of the existing data, compile new data in easily accessible ways and foster collaborative synthesis across regions with a view to tackling some of the “big” questions regarding marine biodiversity in the Indo-Pacific region.

ACKNOWLEDGMENTS

The concept for this study arose from a Catalysis meeting funded by the National Evolutionary Synthesis Center (NESCent) on the Molecular Ecology and Evolution of the Indo-Pacific to EC and CR. This material is based upon work supported by the National Science Foundation through the National Evolutionary Synthesis Center (NESCent) under grant number NSF #EF-0905606. JK is supported by a University of Queensland International and University of Queensland Research Scholarships. Thanks to L Rocha and H Lessios for helpful suggestions during the data collection phase.

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Appendix 1. All species included in the dataset, with their citations and the genetic marker used in the study. Names in black are those species for which species authority was derived from the Integrated Taxonomic Information System, * represents those derived from the World Register of Marine Species and † represents those derived from Fishbase.

Species name and authority	Citations for studies included in this data set	Marker
<i>Acanthaster planci</i> (Linnaeus, 1758)	Benzie 1999, Yasuda et al. 2009	Allozymes, Microsatellites
<i>Acanthochromis polyacanthus</i> (Bleeker, 1855)	Doherty et al. 1995, Miller-Sims et al. 2008	Allozymes, Microsatellites
<i>Acanthopagrus latus</i> (Houttuyn, 1782)	Xia et al. 2008	MtDNA
<i>Acanthurus nigrofasciatus</i> (Forsskål, 1775)	Eble et al. 2011a	MtDNA
<i>Acanthurus nigroris</i> Valenciennes in Cuvier and Valenciennes, 1835	DiBattista et al. 2011	MtDNA
<i>Acanthurus triostegus</i> (Linnaeus, 1758)	Mirams et al. 2011, Planes and Fauvelot 2002	Allozymes, MtDNA
<i>Aipysurus laevis</i> Lacépède, 1804	Lukoschek et al. 2008, Lukoschek et al. 2007	Microsatellites, MtDNA
<i>Amphiprion melanopus</i> Bleeker, 1852	Doherty et al. 1995, Drew et al. 2008	Allozymes, MtDNA
<i>Amphiprion ocellaris</i> Cuvier in Cuvier and Valenciennes, 1830	Timm and Kochzius 2008, Timm et al. 2012	MtDNA, Microsatellites
<i>Anusium pleuronectes</i> (Linnaeus, 1758)*	Mahidol et al. 2007	MtDNA
<i>Apogon doederleini</i> Jordan and Snyder, 1901	Mirams et al. 2011	MtDNA
<i>Asymmetron lucayanum</i> Andrews, 1893	Kon et al. 2006	MtDNA
<i>Aulostomus chinensis</i> (Linnaeus, 1766)	Bowen et al. 2001	MtDNA
<i>Bregus latro</i> (Linnaeus, 1767)†	Lavery et al. 1995	Allozymes
<i>Carcinoscorpius rotundicauda</i> (Latreille, 1802)*	Yap et al. 2011	Allozymes
<i>Carijoa riset</i> (Duchassaing and Michelotti, 1860)	Concepcion et al. 2010	MtDNA, other nuclear markers
<i>Centropyge flavissima</i> (Cuvier in Cuvier and Valenciennes, 1831)	DiBattista et al. 2012	MtDNA
<i>Cephalopholis argus</i> Bloch and Schneider, 1801	Gaither et al. 2011a	MtDNA, other nuclear markers
<i>Chaetodon citrinellus</i> Cuvier in Cuvier and Valenciennes, 1831	Fauvelot and Planes 2002	Allozymes
<i>Chaetodon quadrimaculatus</i> Gray, 1831	Fauvelot and Planes 2002	Allozymes
<i>Chelonia mydas</i> (Linnaeus, 1758)	Bourjica et al. 2007, Dethmers et al. 2006	MtDNA
<i>Chlorurus sordidus</i> (Forsskål, 1775)	Bay et al. 2004, Dudgeon et al. 2000	MtDNA
<i>Chromis atripectoralis</i> Welanders and Schultz, 1951	Doherty et al. 1995	Allozymes
<i>Chromis xanthurus</i> (Bleeker, 1854)	Fauvelot and Planes 2002	Allozymes
<i>Chrysiptera glauca</i> (Cuvier in Cuvier and Valenciennes, 1830)	Fauvelot and Planes 2002	Allozymes
<i>Chrysiptera leucopoma</i> (Cuvier in Cuvier and Valenciennes, 1830)	Lacson and Clark 1995	Allozymes

Appendix 1. Continued.

Species name and authority	Citations for studies included in this data set	Marker
<i>Chrysiptera talboti</i> (Allen, 1975)	Drew et al. 2008	MtDNA
<i>Chthamalus malayensis</i> Pilsbry, 1916 [#]	Tsang et al. 2008	MtDNA
<i>Clavularia koellikeri</i> (Dean, 1927) [#]	Bastidas 2002	Allozymes
<i>Conus chaldaeus</i> (Röding, 1798) [#]	Duda et al. 2012	MtDNA
<i>Conus ebraeus</i> Linnaeus, 1758 [#]	Duda and Lessios 2009	MtDNA
<i>Conus miliaris</i> Hwass in Bruguière, 1792 [#]	Duda and Lee 2009	MtDNA
<i>Conus sanguinolentus</i> Quoy and Gaimard, 1834 [#]	Duda et al. 2012	MtDNA
<i>Coralliophila violacea</i> (Ktner, 1836) [#]	Lin and Liu 2008	Allozymes
<i>Craterocephalus capreoli</i> (Rendahl, 1922)	Johnson et al. 1994	Allozymes
<i>Dasyllus albisella</i> Gill, 1862	Ramon et al. 2008	MtDNA
<i>Dasyllus arianus</i> (Linnaeus, 1758)	Fauvelot and Planes 2002	Allozymes
<i>Dasyllus trimaculatus</i> (Rüppell, 1829)	Mirams et al. 2011	MtDNA
<i>Echinometra mathaei</i> (Blainville, 1825) [#]	Palumbi et al. 1997	MtDNA
<i>Echinometra oblonga</i> (Blainville, 1825) [#]	Palumbi et al. 1997	MtDNA
<i>Echinometra</i> sp. C. first mentioned in Uchida and Shingaki 1985	Palumbi et al. 1997	MtDNA
<i>Eleutheronema tetradactylum</i> (Shaw, 1804)	Horne et al. 2011	MtDNA, Microsatellites
<i>Epinephelus coioides</i> (Hamilton, 1822)	Antoro et al. 2006	Microsatellites
<i>Epinephelus polyphekadion</i> (Bleeker, 1849)	Rhodes et al. 2003	Microsatellites
<i>Euryhalionematooides grandis</i> (Mizelle and Kritsky, 1969) [#] revised to <i>Euryhalionemata grandis</i> Kritsky 2012	Plaisance et al. 2008	MtDNA
<i>Fenneropenaeus indicus</i> (H. Milne-Edwards, 1837)	de Croos and Palsson 2010	MtDNA
<i>Forcipiger flavissimus</i> Jordan and McGregor in Jordan and Evermann, 1898	Fauvelot and Planes 2002	Allozymes
<i>Gnatholepis anjerensis</i> (Bleeker, 1851)	Thacker et al. 2008	Microsatellites
<i>Gnatholepis scapulo stigma</i> Herre, 1953 [#] synonym of <i>G. cauerensis</i> (Bleeker, 1853)	Thacker et al. 2008	Microsatellites
<i>Halichoeres claudia</i> Randall & Rocha, 2009 [#]	Ludt et al. 2012	MtDNA
<i>Halichoeres ornatissimus</i> (Garrett, 1863)	Ludt et al. 2012	MtDNA
<i>Halichoeres trimaculatus</i> (Quoy and Gaimard, 1834)	Ludt et al. 2012	MtDNA

Appendix 1. Continued.

Species name and authority	Citations for studies included in this data set	Marker
<i>Haliotis asinina</i> Linnaeus, 1758	Imron et al. 2007	MtDNA
<i>Haptosquilla glyptocercus</i> (Wood-Mason, 1875) [#]	Barber et al. 2002	MtDNA
<i>Haptosquilla pulchella</i> (Miers, 1880) [#]	Barber et al. 2002	MtDNA
<i>Heliofungia actiniformis</i> (Quoy and Gaimard, 1833)	Knittweis et al. 2009	Other Nuclear Markers
<i>Hippocampus kuda</i> Bleeker, 1852	Teske et al. 2005	MtDNA
<i>Holothuria (Halodeima) atra</i> Jaeger, 1833	Uthicke et al. 2001	Allozymes
<i>Holothuria (Microthele) nobilis</i> (Selenka, 1867)	Uthicke and Benzie 2003	MtDNA
<i>Holothuria (Meristylia) scabra</i> Jaeger, 1833	Uthicke and Benzie 2001, Uthicke and Purcell 2004	Allozymes
<i>Lates calcarifer</i> (Bloch, 1790)	Chenoweth et al. 1998, Yue et al. 2009	MtDNA, Microsatellites
<i>Lethrinus miniatus</i> (Forster in Bloch and Schneider, 1801)	van Herwerden et al. 2009a, van Herwerden et al. 2003	Microsatellites, MtDNA
<i>Linckia laevigata</i> (Linnaeus, 1758) [#]	Crandall et al. 2008b, Kochzius et al. 2009, Williams and Benzie 1993, 1996	MtDNA, Allozymes
<i>Lutjanus erythropterus</i> Bloch, 1790	Zhang et al. 2006	MtDNA
<i>Lutjanus fulvus</i> (Forster in Bloch and Schneider, 1801)	Gaither et al. 2010	MtDNA
<i>Lutjanus kasmira</i> (Forsskål, 1775)	Gaither et al. 2010	MtDNA
<i>Lutjanus sebae</i> (Cuvier, 1816)	van Herwerden et al. 2009a	MtDNA
<i>Penaeus japonicus</i> (Bate, 1888) <small>synonym of <i>Marsupenaeus japonicus</i></small>	Tsoi et al. 2007	Microsatellites
<i>Mugil cephalus</i> Linnaeus, 1758	Livi et al. 2011	MtDNA
<i>Myripristis berndti</i> Jordan and Evermann, 1903	Craig et al. 2007, Muths et al. 2011	MtDNA, Microsatellites
<i>Naso brevirostris</i> (Cuvier, 1829)	Horne et al. 2008	MtDNA
<i>Naso vlamingii</i> (Valenciennes in Cuvier and Valenciennes, 1835)	Klanten et al. 2007	MtDNA
<i>Negaprion acutidens</i> (Ruppell, 1837)	Schultz et al. 2008	MtDNA, Microsatellites
<i>Nerita albicilla</i> Linnaeus, 1758 [#]	Crandall et al. 2008a	MtDNA
<i>Nerita plicata</i> Linnaeus, 1758 [#]	Crandall et al. 2008a	MtDNA
<i>Penaeus monodon</i> Fabricius, 1798	Duda and Palumbi 1999, Mandal et al. 2012	Other nuclear markers, Microsatellites
<i>Periclimenes soror</i> Nobili, 1904	Crandall et al. 2008b	MtDNA
<i>Perna viridis</i> (Linnaeus, 1758) [#]	Prakoon et al. 2010, Yap et al. 2004	Microsatellites, Allozymes

Appendix 1. Continued.

Species name and authority	Citations for studies included in this data set	Marker
<i>Phycomenes zostericola</i> Bruce, 2008 [#]	Haig et al. 2010	MtDNA
<i>Pinctada maxima</i> (Jameson, 1901) [#]	Lind et al. 2007	Microsatellites
<i>Plectorhynchus flavomaculatus</i> (Cuvier in Cuvier and Valenciennes, 1830)	Han et al. 2008	MtDNA
<i>Plectroglyphidodon dickii</i> (Liénard, 1839)	Fauvelot and Planes 2002	Allozymes
<i>Plectropomus leopardus</i> (Lacépède, 1802)	Van Herwerden et al. 2009b	MtDNA
<i>Polynemus sheridani</i> MacLeay, 1884 [#] synonym of <i>Polydactylus macrolepis</i> (Günther, 1867)	Chenoweth and Hughes 2003	MtDNA
<i>Pomacentrus coelestis</i> Jordan and Starks, 1901	Liu et al. 2008, Mirams et al. 2011	MtDNA
<i>Pomacentrus moluccensis</i> Bleeker, 1853	Drew et al. 2008	MtDNA
<i>Pomacentrus pavo</i> (Bloch, 1787)	10.1007/s00227-002-0869-7	Allozymes
<i>Pristipomoides filamentosus</i> (Valenciennes in Cuvier and Valenciennes, 1830)	Gaither et al. 2011b	MtDNA, Microsatellites
<i>Pristipomoides multidentis</i> (Day, 1871)	Ovenden et al. 2002, Ovenden et al. 2004	MtDNA
<i>Protoreaster nodosus</i> (Linnaeus, 1758) [#]	Crandall et al. 2008b	MtDNA
<i>Pterapogon kauderni</i> Koumans, 1933	Bernardi and Vagelli 2004, Hoffman et al. 2005, Vagelli et al. 2009	MtDNA, Microsatellites
<i>Pterocaesio chrysozona</i> (Cuvier in Cuvier and Valenciennes, 1830)	Doherty et al. 1995	Allozymes
<i>Scarus frenatus</i> Lacépède, 1802	Dudgeon et al. 2000	MtDNA
<i>Scarus ghobban</i> Forsskål, 1775	Visram et al. 2010	MtDNA
<i>Scarus psittacus</i> Forsskål, 1775	Winters et al. 2010	MtDNA
<i>Scarus rubroviolaceus</i> Bleeker, 1847	Fitzpatrick et al. 2011	Microsatellites
<i>Scylla serrata</i> (Forsskål, 1775)	Fratini and Vannini 2002, Gopurenko and Hughes 2002, Gopurenko 1999	MtDNA
<i>Sicyopterus aienensis</i> Keith, Watson & Marquet, 2004 [‡]	Lord et al. 2012	MtDNA
<i>Sicyopterus lagocephalus</i> (Pallas, 1770)	Hoareau et al. 2012, Lord et al. 2012	MtDNA
<i>Sicyopterus sarasini</i> Weber and de Beaufort, 1915	Lord et al. 2012	MtDNA
<i>Siganus argenteus</i> (Quoy and Gaimard, 1825)	Magsino and Junio-Meñez 2008	Allozymes
<i>Siganus fuscescens</i> (Houttuyn, 1782)	Magsino and Junio-Meñez 2008, Ravago-Gotanco and Junio-Menez 2010	Allozymes, MtDNA

Appendix 1. Continued.

Species name and authority	Citations for studies included in this data set	Marker
<i>Siganus guttatus</i> (Bloch, 1787)	Iwamoto et al. 2009	MtDNA
<i>Simularia flexibilis</i> (Quoy and Gaimard, 1833) [#]	Bastidas et al. 2001	Allozymes
<i>Sphyræna barracuda</i> (Edwards in Catesby, 1771)	Daly-Engel et al. 2012	MtDNA
<i>Segastes fasciolatus</i> (Ogilby, 1889)	Ramon et al. 2008	MtDNA
<i>Segastes nigricans</i> (Lacépède, 1802)	Doherty et al. 1995	Allozymes
<i>Segostoma fasciatum</i> (Hermann, 1783)	Dudgeon et al. 2009	MtDNA, Microsatellites
<i>Stichopus chloronotus</i> Brandt, 1835 [#]	Uthicke et al. 1999, Uthicke et al. 2001	Allozymes
<i>Thyca crystallina</i> (Gould, 1846) [#]	Crandall et al. 2008b, Kochzius et al. 2009	MtDNA
<i>Tridacna crocea</i> Lamarck, 1819 [#]	DeBoer et al. 2008, Kochzius and Nuryanto 2008	MtDNA
<i>Tridacna derasa</i> (Röding, 1798) [#]	Macaranas et al. 1992	Allozymes
<i>Tridacna gigas</i> (Linnaeus, 1758) [#]	Benzie and Williams 1995	Allozymes
<i>Tridacna maxima</i> (Röding, 1798) [#]	Benzie and Williams 1997, Nuryanto and Kochzius 2009	Allozymes, MtDNA
<i>Zebrasoma flavescens</i> (Bennett, 1828)	Eble et al. 2011b	MtDNA, Microsatellites